Behavioral reactions of brown bears to approaching humans in Fennoscandia

Moen, Gro Kvelprud

2019

Moen , G K , Ordiz , A , Kindberg , J , Swenson , J E , Sundell , J & Stoen , O-G 2019 , ' Behavioral reactions of brown bears to approaching humans in Fennoscandia ' , Écoscience , vol. 26 , no. 1 , pp. 23-33 . https://doi.org/10.1080/11956860.2018.1513387

http://hdl.handle.net/10138/307591
https://doi.org/10.1080/11956860.2018.1513387

unspecified
acceptedVersion

Behavioral reactions of brown bears to approaching humans in Fennoscandia

Authors and affiliations

Gro Kvelprud Moen[1,*], Andrés Ordiz[1], Jonas Kindberg[2,3], Jon E. Swenson[1,3], Janne Sundell[4], Ole-Gunnar Støen[3,1,*]

[1]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Postbox 5003, NO-1432 Ås, Norway

[2]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

[3]Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

[4]University of Helsinki, Lammi Biological Station, Pääjärventie 320, FI-16900 Lammi, Finland.

* Corresponding authors. Email address: gro.moen@nmbu.no; Tel number: +4799721009. Email address: ole.stoen@nina.no; Tel number: +4797119945.

Summary

Human disturbance causes behavioral responses in wildlife, including large carnivores. Previous research in Scandinavia has documented that brown bears (*Ursus arctos*) show a variety of behavioral reactions to different human activities. We investigated how proximity to human settlements and roads, as proxies of human influence, affected brown bears' reactions to encountering humans. We analyzed experimental approaches to GPS collared bears, 18 males and 23 single females, in Sweden (n = 148 approaches) and Finland (n = 33), conducted between 2004 and 2012. The bears in Finland inhabited areas with higher human density compared to Sweden. However, the proportion of bears staying or moving when approached and the flight initiation distances were similar in both countries. In Sweden, the flight responses were not dependent on human densities or roads inside the bears' home ranges or the distances from the bears to roads and settlements. Brown bears in Fennoscandia live in areas with relatively low human population densities, but in many areas with high forestry road densities. Our results show that bears' flight reactions were consistent between areas, which is an important message for management, reinforcing previous studies that have documented human avoidance by bears at very different spatial and temporal scales.

Keywords: experimental human disturbance, Finland, flight initiation distance, flight responses, human density, road density, Sweden

Introduction

Wildlife generally react to and avoid human activities. However, behavioral responses vary in relation to factors such as the individuals' previous experience, physical condition, age, degree of gregariousness, antipredator strategies, type of disturbance, and time of day when it occurs (e.g., Whittaker and Knight 1998, Beale and Monaghan 2004a, Stankowich 2008,

Vincze et al. 2016, Tablado and Jenni 2017). Human disturbance can have short- and long-term effects, such as changes in distribution and activity patterns, and reduced breeding success (Beale and Monaghan 2004b, Stankowich 2008 and references therein).

Moving away from or avoiding areas with human activity is indeed an antipredator response, with disturbance perceived as predation risk by the responding animal (e.g., Gill et al. 1996, Lima 1998, Frid and Dill 2002). Antipredator responses reduce risk and are therefore crucial in modulating animal behavior (e.g., Deecke et al. 2002). Nevertheless, risk avoidance implies costs, which animals try to minimize while maximizing survival (e.g., Gill et al. 1996, Lima 1998).

Mammalian carnivores can be especially vulnerable to human disturbance (e.g., George and Crooks 2006). Large carnivores, such as brown bears (*Ursus arctos*), show spatial and temporal reactions to a variety of human activities across their wide distribution range in North America (e.g., Gibeau et al. 2002, Nielsen et al. 2004, Rode et al. 2006) and Europe (e.g., Naves et al. 2003, Nellemann et al. 2007, Ordiz et al. 2017). In Scandinavia, as elsewhere, most brown bear mortality is caused by humans (Sahlén et al. 2006, Bischof et al. 2009) and mortality risk is higher closer to villages and roads (Steyaert et al. 2016). Not surprisingly, brown bears generally select for rugged areas far from people (Nellemann et al. 2007). Bears' resting sites are concealed by denser vegetation when bears are closer to villages and during daytime compared to nighttime, suggesting that bears perceive and react to proximity to people, especially in summer-autumn, when human activities outdoors are most common (Ordiz et al. 2011). Bears' stress levels are also higher when they are closer to humans (Støen et al. 2015).

Brown bears have been expanding in Scandinavia in the last century following a severe population decline, from approximately 130 bears around 1930 to ~3,000 bears in recent times (Swenson et al. 1995, Swenson et al. 2017), and some people express concern about

65 human safety in the forest. Similarly, in Finland there were only about 150 bears by the
66 1960's (Pulliainen 1983), and the population reached 1,150-1,950 bears in 2009 (Wikman
67 2010, Kopatz et al. 2014). Therefore, to better understand bear behavior and to inform
68 management agencies and the public about the reactions of bears to casual encounters with
69 outdoor users (hikers, berry or mushroom pickers, hunters, etc.), we have conducted several
70 studies in Sweden that included experimental approaches to radio-collared bears. Most bears
71 react by moving away, which holds for both single bears (Moen et al. 2012) and females with
72 cubs (Sahlén et al. 2015). After the encounters, bears become more nocturnal (Ordiz et al.
73 2013), as they do when bear hunting seasons start (Ordiz et al. 2012), and when they live in
74 areas with higher road densities (Ordiz et al. 2014). That is, the behavioral reaction of the
75 bears goes beyond their initial flight after encountering a person, which can change bears'
76 daily activity patterns for several days (Ordiz et al. 2013).
77 Whereas the research summarized above shows a solid pattern of bears' avoidance of
78 people, it was conducted in areas with low human densities. There is a need for research on
79 bear reactions to humans also in areas with higher human densities, because the range of
80 brown bears has been expanding in Fennoscandia, with bears moving into more human-
81 dominated landscapes (Swenson et al. 1998, Kojola and Heikkinen 2006). It is possible that
82 bears relax their behavioral responses if they encounter humans more often and eventually
83 habituate to their proximity. This could in turn make encounters with bears more dangerous, if
84 they do not move away as consistently as we have documented so far (Moen et al. 2012,
85 Sahlén et al. 2015).
86 In this study, we have conducted experimental approaches of radio-collared bears in
87 Sweden and Finland to assess whether bears' behavioral responses, i.e., flight reactions,
88 change in relation to the level of human activity. We used distance to roads and human
89 settlements from the bears' initial sites and the densities of human population and roads in

bears' home ranges as proxies for human activity. We also controlled for variables that influence the bears' flight reactions, i.e., bear behavior (if it was active or passive when approached), vegetation concealment, season of the year, and individual characteristics of the bears (Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2015). As previous studies show that brown bears in Scandinavia avoid humans on different scales, we did not expect to see a reduced behavioral response of bears encountered by people due to living in areas with higher human or road densities, but a consistent pattern of human avoidance by the bears.

Methods

Study areas

The experimental approaches were conducted in Sweden and Finland. The study area in southcentral Sweden (61.5°N 15° E, Gävleborg and Dalarna counties) consists of bogs and heavily managed coniferous forest of mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). There are few main roads in the area, but a dense network of gravel roads (1.0 ± 0.8 km/km^2, mean ± SD) (Road map: Swedish National Land Survey). The human population in the area is low, 3.6 - 6.2 inhabitants/km^2 in the four municipalities where the study was conducted (Statistics Sweden). The whole study area is located below the timberline, which is at approximately 750 m a.s.l. (Dahle and Swenson 2003). Temperatures in the study area average -7° C in January and 15° C in July (Swedish Meteorological and Hydrological Institute 2017a, b). The density of bears in the study area was estimated to ~30 bears/1000 km^2 (Solberg et al. 2006).

The study area in central and southeastern Finland (62.5°N 27°E) also consists of bogs and managed coniferous forest of Scots pine and Norway spruce. Altitudes range from 75 to 200 m a.s.l, all below the timberline. Temperatures average -8° C in January and 17° C in July (Finnish Meteorological Institute). There is a dense network of roads in the area (1.5 ± 1.1

km/km^2) (National Land Survey of Finland), and the average human population is higher than in the Swedish study area (11.3 - 16.2 inhabitants/km^2) (Statistics Finland 2008). An estimate of the bear density in the study area is ≥ 6 bears/1000 km^2 (Wikman 2010). The bears are hunted in the fall in both areas, with hunting quotas averaging about 10% of the estimated populations in recent years, i.e., ~300 bears are annually harvested in Sweden (National Veterinary Institute 2017) and ~100 in Finland (The Finnish Wildlife Agency 2017).

Bears and the experimental approaches

We analyzed 148 experimental approaches between humans and adult solitary brown bears (9 males and 21 females) conducted in Sweden from 2006 to 2009, and 33 approaches on solitary bears (9 males and 2 females) carried out in the Finnish study area from 2004 to 2012. The bears were either followed from birth, being captured with previously known mothers, or their age was determined through cross-section of the premolar roots (Matson et al. 1993). Bears were from four to twenty years old in Sweden, and three to eleven years old in Finland. In Sweden, we approached the bears between one and six times per season, with a minimum of 13 days and maximum of 92 days between each approach. Most of the bears in Sweden were approached during one season (n = 18), although some were approached during two (n = 10) or three seasons (n = 2). We approached the bears in Finland with a minimum of seven days and maximum of 50 days between the approaches. The bears in Finland were approached between one and six times per season, during one (n = 9) or three (n = 2) seasons.

The bears were captured and equipped with GPS Plus-3 or GPS Pro-4 neck collars (VECTRONIC Aerospace GmbH, Berlin, Germany) and a VHF transmitter implant (IMP 400L) (Telonics, USA) in Sweden, and Tracker GSM/GPS without VHF (Tracker Inc., Oulunsalo, Finland) in Finland (see Sundell et al. (2006) and Arnemo et al. (2007) for details). The females in Finland were equipped with the same collar as the Swedish bears. Handling was approved by the Swedish Ethical Committee on Animal Research and the Swedish

140 Environmental Protection Agency in Sweden, and the National Animal Experiment Board and
141 the Finnish Ministry of Agriculture and Forestry in Finland.
142 On the day of the approach in Sweden, the bears' GPS collars were scheduled to send
143 positions every minute for three hours; one hour before the approach started and two hours
144 after. The position data in Sweden was collected into the Wireless Remote Animal
145 Monitoring (Dettki et al. 2013) database system for data validation and management. In
146 Finland, the collars were scheduled to send positions every 25 seconds at the start of the
147 approach, resulting in a poorer determination of pre-encounter behavior than in Sweden, and
148 the interval of positions was gradually increased to 24 hours after the bear was passed by the
149 observers. The females' collars were scheduled to send positions every minute. The
150 approaches in Sweden were conducted between 10:00 and 16:00 local time, when most bears
151 usually rest (Moe et al. 2007). The approaches in Finland were conducted between 08:00 and
152 19:00 local time. Prior to the approaches, the bears in Sweden were located based on
153 triangulation of the VHF-signals from the neck collars and the implant. In Finland, bears'
154 locations before the approach were obtained from GPS positions in real time. The approaches
155 were conducted by one to six people (1.9 ± 0.7 observers), hereafter referred to as the
156 observers, who mimicked hikers and talked to each other during the encounters. If only one
157 observer conducted the approach, this person talked to him- or herself during the approach.
158 The observers started the approaches 841 ± 336 m from the bear in Sweden and 952 ± 455 m
159 in Finland, walked towards it, passing the initial sites at 57 ± 67 m in Sweden and 52 ± 21 m
160 in Finland (the goal was passing the bears at approximately 50 m). During the approaches, the
161 bear's location and movement were monitored using VHF-tracking equipment in Sweden and
162 by observing the GPS positions on a computer by another observer who was in telephone
163 contact with the observers in the field in Finland. After passing the bear, the observers
164 continued walking away (approximately 500 m), keeping a distance to the bear to avoid

disturbing it a second time. The track of the observers in Sweden was registered with positions every 10 m using a hand-held GPS receiver and the observers' track in Finland was recorded with a GPS GSM device, similar to the bear collar (Benefon ESC!, Benefon Oyj, Salo, Finland), set for sending positions every 20 seconds.

Based on the GPS positions, bears were categorized as either 'passive', most typically resting in a daybed, or 'active', e.g., foraging or moving around. If the diameter of the positions in the control period, from start of minute positioning to the start of the approach, did not exceed 70 m (min: 6 m, max: 68 m), the bears were judged as 'passive' (Moen et al. 2012, Sahlén et al. 2015). Bears were considered 'active' if the diameter exceeded 70 m (min; 80 m, max; 1728 m), and the positions indicated movement in the time before approach (Moen et al. 2012, Sahlén et al. 2015). This was visually checked in ArcGIS 10.1 (ESRI 2012). Some bears changed their activity during the control period, and the new activity level was the basis for the analysis.

Site visits after encounters

In Sweden, field personnel visited both the initial site (IS), where the bear stayed prior to the encounter, and the second site (SS), where the bear settled down after being disturbed, a few days after the approaches were conducted. We located daybeds, verified by presence of bear hair, and used this as the center of the IS of the passive bears and SS. For passive bears without confirmed daybeds, the center of the cluster of GPS positions was defined as the IS, and the last position before the approach started was defined as the IS for active bears. As a proxy for concealment, the horizontal vegetation cover was measured as sighting distance (Ordiz et al. 2009) in both IS and SS. The average sighting distance of the four cardinal

187 directions gave a sighting distance for each of the sites (see Ordiz et al. (2009) and Moen et
188 al. (2012) for more details).

189 **Data management and analysis**

190 We calculated the speed between the bears' successive GPS positions and identified the
191 reactions to the encounters using statistical quality control (Montgomery 2005) and an
192 estimated upper control limit (UCL) for the control period, as described in Moen et al. (2012);
193 flight reaction identified for passive bears when movement was > 33.5 m/min (> 2.01 km/h),
194 and for active bears with movement > 101.3 m/min (> 6.08 km/h). The flight initiation
195 distance (FID) was defined as the distance from the observer to the bears' last position prior
196 to an increased movement, i.e., where the speed between the bear's two successive GPS
197 positions exceeded the activity-specific UCL and the bear left the initial site. This was also
198 checked visually in ArcGIS 10.1 (ESRI 2012). We did not include approaches where the
199 positions were missing for more than two minutes around the disturbance event; therefore, 19
200 approaches were excluded from the analysis of FID. Three bears left their IS without
201 exceeding the activity-specific UCL, hence no FID was registered.

202 Passing distance was calculated as the shortest distance between the IS and the observer,
203 regardless of whether the bear was still in the IS when it was passed by the observer. The
204 minimum distance from the observer to the bear (distance to observer) was calculated as the
205 shortest distance from the observer to the bear during the encounter. If the bear was at the IS,
206 distance to observer was calculated as distance from observer to IS. When a FID was recorded
207 and the bear settled down in a SS before the end of the scheduled minute positioning, the
208 distance between the position of FID and SS was defined as distance moved (DM). The
209 difference between time of FID and the first position in SS was defined as the time the bears
210 spent moving after disturbance (TSM). The method of data collection was different in
211 Finland, which resulted in fewer GPS positions after the observer passed the bears' initial

212 sites. DM and TSM were therefore only calculated for the bears in the Swedish study area. In
213 Sweden, two bears were encountered twice during one experiment, and DM and TSM were
214 not included in the analysis. One bear left after the end of the encounter, and this was not
215 included in the analysis of FID, DM, or TSM. In cases where the positioning prior to the
216 approaches was insufficient, we could not decide on the activity level of the bear, and the
217 encounters were not included in the analysis of FID, DM or TSM.

218 We used linear regression to analyze which variables affected whether bears stayed or
219 moved when encountered, and their FID, DM, and TSM in Sweden. We included horizontal
220 vegetation cover (sighting distance) at IS, the bears' age and sex, activity pattern prior to the
221 encounter, season, number of observers, and passing distance or distance to observer as
222 potential explanatory variables (Table 1), following previous studies (Moen et al. 2012, Ordiz
223 et al. 2013, Sahlén et al. 2015). Horizontal vegetation cover (sighting distance) at SS was also
224 included in the analysis of DM and TSM. The annual study periods were divided into pre-
225 berry season (< 15 July) and berry season (≥ 15 July), which accounts for seasonality in bear
226 phenology and intensity of outdoor human activities (Ordiz et al. 2013).

227 In addition, variables that could describe how bears perceive human disturbance in the area
228 around the IS and in their home ranges were included (Table 1). Based on maps from
229 Statistics Sweden and Swedish National Land Survey in Sweden, and National Land Survey
230 of Finland in Finland, we calculated the distances from the bears' IS and SS to the closest
231 road and the closest settlement using ArcGis 10.1 (ESRI 2012). Distance from IS and SS to
232 the closest settlement was highly correlated ($r > 0.90$), hence we only used distance from IS to
233 settlements in the regression models for DM and TSM.

234 The R package 'adehabitatHR' (Calenge 2006) was used to calculate the home range
235 kernels for each bear and year, based on half-hour GPS positions from the bears, using "href"
236 as the smoothing parameter (Calenge 2015). We calculated the home range kernels with

237 percentage levels of 50, 60, 70, 80, 90, and 95%. Densities of roads (km road/km^2) and human
238 population (inhabitants/km^2) were identified within each home range level using PostGIS
239 2.2.2 (http://postgis.net/) and GEOSTAT 1 km^2 population grid for 2006 (Eurostat) for density
240 of inhabitants and property map from 2016 (Swedish National Land Survey) for road density.
241 We could not identify a significant difference in the variation of road density between the
242 different levels of home range kernels (Levene's test: $p = 0.63$) (R package 'car': Fox and
243 Weisberg 2011) (50% level: 1.06 ± 0.03 km road/km^2 (mean ± SE), 60% level: 1.09 ± 0.03
244 km road/km^2, 70% level: 1.12 ± 0.03 km road/km^2, 80% level: 1.12 ± 0.03 km road/km^2, 90%
245 level: 1.14 ± 0.02 km road/km^2, 95% level: 1.14 ± 0.02 km road/km^2), so we used the 95%
246 home range kernels in the analysis. Similarly, we could not identify a significant difference in
247 the variation of human population density between the different levels of home range kernels
248 (Levene's test: $p = 0.96$) (50% level: 0.14 ± 0.03 inhabitants/km^2 (mean ± SE), 60% level:
249 0.17 ± 0.05 inhabitants/km^2, 70% level: 0.18 ± 0.05 inhabitants/km^2, 80% level: 0.19 ± 0.04
250 inhabitants/km^2, 90% level: 0.2 ± 0.04 inhabitants/km^2, 95% level: 0.22 ± 0.06
251 inhabitants/km^2), and we also used the 95% home range kernel here.

252 We compared how close the bears' ISs were to settlements and roads in Sweden and
253 Finland. We also tested if bears' FIDs where similar or not, and if approached bears stayed or
254 moved away similarly in both countries. However, the method of data collection in Finland
255 was different, which did not allow us to identify the bears' home ranges, hence we did not
256 calculate the densities of roads or human population within the home ranges, and we did not
257 include the data from Finland in the regression models to explore which variables affected the
258 flight reactions of bears.

259 Table 1. Overview of the potential explanatory variables included in the regression models to analyze
260 flight reactions of brown bears in Sweden. The response variables were stayed or moved, flight
261 initiation distance (FID), distance moved after being disturbed (DM), and time spent moving after
262 being disturbed (TSM). Activity = activity of the bear prior to the encounter; passive (0) or active (1),
263 Age = age of bear in years, Sex = sex of the bear; male (0) or female (1), Sighting distance in IS or SS
264 = Sighting distance at initial site (IS) or second site (SS) in m, i.e., horizontal vegetation cover at the
265 site, Season = pre-berry season (0) or berry season (1), Passing distance = closest distance from

observer to initial site in m, Distance to observer = minimum distance between observer and bear during the encounter in m, Number of observers = number of observers conducting the encounter, Distance to settlements from IS = distance from initial site to the closest settlement in m, Distance to road from IS or SS = distance from initial site (IS) or second site (SS) to the closest road in m, Road HR = km road/km^2 within the bear's 95% home range kernel, Human HR = density of human population as inhabitants/km^2 within the bear's 95% home range kernel.

Response variable	Exploratory variables
Stayed or moved	Activity + Age + Sex + Sighting distance in IS + Season + Number of observers + Distance to observer + Distance to settlements from IS + Distance to road from IS + Road HR + Human HR
FID	Activity + Age + Sex + Sighting distance in IS + Season + Number of observers + Passing distance + Distance to settlements from IS + Distance to road from IS + Road HR + Human HR
DM and TSM	Activity + Age + Sex + Sighting distance in IS + Sighting distance in SS + Season + Number of observers + Distance to observer + Distance to settlements from IS + Distance to road from IS + Distance to road from SS + Road HR + Human HR

We used generalized linear mixed models with a binomial link function in 'glmer' in R package 'lme4' (Bates et al. 2015) to analyze which factors explained that bears stayed or moved when encountered. We used linear mixed models with function 'lmer' in R package 'lme4' (Bates et al. 2015) to analyze FID, DM, and TSM, which were all log transformed to account for left-skewed distributions. Using the function 'dredge' in R package 'MuMIn' (Barton 2017), possible candidate models for each of the flight responses were identified after standardizing the continuous variables to a mean of 0 and SD of 1 (Grueber et al. 2011) using package 'standardize' (Eager 2017). The random factor bear ID was used for all of the response variables. We calculated variance inflation factors (VIF) for the regression models for the different response variables, and they did not show sign of multicollinearity among variables. We did not identify any correlation between the covariates at $r > 0.6$.

Because there were several candidate models with $\Delta AICc < 2$ for the models with the response variables stayed or moved, DM and TSM, we averaged each set of models with the function 'model.avg' in package 'MuMIn' (Barton 2017), and we report the outcome of the full average models (Burnham and Anderson 2002, Grueber et al. 2011). We interpreted the direction of the effects of the parameters included in the models with the 95% confidence

intervals (CI) of the effect sizes (β). When the 95% CI did not include zero, the effect had a positive or negative effect on the response variable (Arnold 2010). We used R software (R Core Team 2018) for all statistical analysis.

Results

In Sweden, the bears' ISs were 20.0 ± 8.6 km (mean ± SD) (n = 147) from the closest settlement, and 0.35 ± 0.21 km from the closest road. In Finland, the bears' ISs were 11.8 ± 6.2 km (n = 20) from the closest settlement, and 0.25 ± 0.13 km from the closest road, i.e., distances from IS to settlements (Wilcoxon rank-sum test: W = 2256, p-value = 0.0001) and distances from IS to roads (Wilcoxon rank-sum test: W = 1876, p-value = 0.046) were shorter in Finland than in Sweden. On average, the home range kernels (95%) of the bears approached in Sweden had a density of 1.1 ± 0.1 km road/km^2 and a human population density of 0.2 ± 0.4 inhabitants/km^2.

In Sweden, bears stayed in their IS in 40 encounters and moved away in 107, and they stayed in seven cases and moved away in 16 in Finland. The proportion of bears that stayed and moved was not significantly different in Sweden and Finland (Fisher's Exact test for count data: p-value = 0.803, n = 170). In Sweden, bears moved away more often during the berry season than before, and with a higher number of approaching observers. The 95% CI of the effect estimates of other variables included the zero value, and therefore the direction of the effect on the response was unclear (Tables 2 and 1A). Here we provide the results of the model averaging for each response variable. The sets of top candidate models (ΔAICc < 2 compared to the model with the lowest AICc for each response variable) are in Appendix 1.

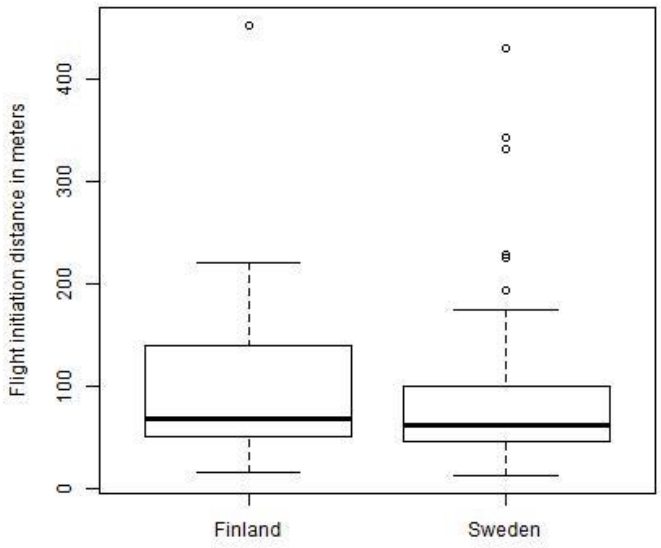
Table 2. Results from the generalized linear mixed regression (binomial link function) explaining the factors that influenced whether bears stayed (0) or moved (1), with test statistics (full average) for the averaged models with ΔAICc < 2. The bears were experimentally approached in southcentral Sweden in 2006-2009 (n = 118). The continuous variables are scaled to 1 SD. See Table 1 for explanation of

316 the variables. β is the effect size and SE the standard error.
317

Parameter	β	SE	95% CI
Intercept	-1.631	0.864	(-3.342, 0.080)
Season (pre-berry season = 0, berry season = 1)	1.659	0.502	(0.664, 2.654)
Number of observers	0.762	0.382	(0.006, 1.519)
Distance to observer	-0.093	0.186	(-0.459, 0.274)
Human HR	0.068	0.180	(-0.286, 0.422)
Road HR	0.050	0.144	(-0.234, 0.334)
Distance to road from IS	0.014	0.082	(-0.148, 0.176)
Activity (passive = 0, active = 1)	-0.037	0.232	(-0.494, 0.421)

318

319 Average FID for bears that left before the observer passed the bear was 87 m ± 72 m (median
320 = 63 m, n = 78) in Sweden and 120 m ± 129 m (median = 69 m, n = 11) in Finland. FID was
321 not significantly different in the two countries (Wilcoxon rank-sum test: W = 393, p-value =
322 0.658) (Fig. 1). FID for bears in Sweden increased with longer sighting distance, i.e., less
323 concealment at initial sites and longer passing distance (Table 3).



324

325 Figure 1: Distribution of flight initiation distances (in meters) in Finland (n = 11) and Sweden (n = 78)
326 following experimental approaches conducted from 2004 to 2012 on radio-collared brown bears, when
327 the bears left their initial sites before the observers passed them.
328

329 Table 3. Results from the linear mixed regression of flight initiation distance (FID), with test statistics
330 for the model with ΔAICc < 2. The bears were experimentally approached in southcentral Sweden in
331 2006-2009 (n = 72). FID was log transformed. The continuous variables were scaled to 1 SD. See

Table 1 for explanation of the variables. β is the effect size and SE the standard error.

	AICc	ΔAICc	Model weight	β	SE	95% CI
Model: FID ~ Sighting distance in IS + Passing distance	190.2	0.00	1			
Intercept				-0.001	0.106	(-0.211, 0.207)
Sighting distance in IS				0.342	0.097	(0.152, 0.534)
Passing distance				0.453	0.094	(0.269, 0.642)

Bears in Sweden that moved away from the initial site when encountered, moved on average 1,002 ± 809 m (n = 87) in 22 ± 21 min (n = 69). DM was longer for active than for passive bears, with more concealment in IS, and with more observers (Tables 4 and 2A). For TSM, the CI of the variables included in the model included zero, i.e., none of the variables had a clearly negative or positive effect on the response (Tables 5 and 3A).

Table 4. Results from the linear mixed regression of distance moved (DM), with test statistics (full average) for the averaged models with ΔAICc < 2. The bears were experimentally approached in southcentral Sweden in 2006-2009 (n = 71). DM is log transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the variables. β is the effect size and SE the standard error.

Parameter	β	SE	95% CI
Intercept	-1.186	0.419	(-2.018, -0.354)
Activity (passive = 0, active = 1)	0.918	0.324	(0.270, 1.566)
Sex (male = 0, female = 1)	0.410	0.315	(-0.213, 1.032)
Sighting distance in IS	-0.326	0.112	(-0.550, -0.102)
Number of observers	0.378	0.130	(0.118, 0.639)
Season (pre-berry season = 0, berry season = 1)	0.066	0.179	(-0.288, 0.421)

Table 5. Results from the linear mixed regression of time spent moving after disturbance (TSM), with test statistics (full average) for the averaged models with ΔAICc < 2. The bears were experimentally approached in southcentral Sweden in 2006-2009 (n = 63). TSM is log transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the variables. β is the effect size and SE the standard error.

Parameter	β	SE	95% CI
Intercept	2.217	0.405	(1.415, 3.019)
Number of observers	0.246	0.168	(-0.086, 0.579)
Sighting distance in IS	-0.062	0.117	(-0.293, 0.169)
Sex (male = 0, female = 1)	0.055	0.172	(-0.285, 0.396)

Discussion

355 Our experimental approaches of brown bears in Sweden and Finland showed similar flight
356 reactions by the bears in both countries. The distance from bears' initial sites to settlements
357 and roads were shorter in Finland than in Sweden, reflecting the higher densities of human
358 population and roads in the study area in Finland. Nevertheless, the bears' responses showed a
359 consistent pattern of human avoidance. The proportion of bears that stayed at their initial sites
360 and the FID of the bears that moved were not different in Sweden and Finland. This
361 consistency in bear behavior can be explained by several reasons. First, the bear populations
362 in Sweden and Finland show similar historical trends, with recent population recovery after
363 centuries of intense persecution (Pulliainen 1983, Swenson et al. 1995, Wikman 2010, Kopatz
364 et al. 2014, Swenson et al. 2017). Second, bears are managed as game species in both
365 countries, with similar annual levels of legal hunting (National Veterinary Institute 2017, The
366 Finnish Wildlife Agency 2017), as explained in Methods. Third, it has also been suggested
367 that some flight responses to disturbance, e.g., FID, are species-specific and therefore
368 responses may be predictable and repeatable at different sites (Blumstein et al. 2003). In
369 addition, large carnivores living in human-dominated landscapes are generally elusive, likely
370 as a response to long-term human persecution, and European bears are no exception (Ordiz et
371 al. 2011, Zedrosser et al. 2011).
372 We were able to analyze, at a finer scale, if human-related variables influenced the bears'
373 behavioral responses when they were approached in Sweden. The human-related variables
374 road density and human population density inside home ranges of the approached bears, and
375 distances to roads from the bears' initial sites when they were approached, were retained in
376 the final, averaged model for the flight response variable stayed/moved (Table 2). However,
377 the 95% CI of the effect estimates of those variables included zero, i.e., they explained some
378 variation in the bears' flight response, but the direction of their effects was not clear. The
379 human population density inside the home ranges of the approached bears in Sweden (0.2 ±

380 0.4 inhabitants/km^2) was lower than the average human population density in the study area
381 generally (3.6 - 6.2 inhabitants/km^2). However, the road density inside the home ranges (1.1 ±
382 0.1 km road/km^2) was virtually identical to the average values in the study area (1.0 ± 0.8 km
383 road/ km^2). The low human densities and the lack of variation in road density may help
384 explain the low effect of the human-related variables in these analyses. Regarding human
385 density, bears avoid humans on the landscape scale, residing far from people (Nellemann et
386 al. 2007), even if human density is generally low in our study area. Regarding road density, it
387 reflects the dense network of forest roads built over the years to harvest the coniferous forest,
388 and these roads are virtually impossible for bears to avoid, given their large home ranges.
389 Previous research helps interpret these results as well. Whereas proximity to settlements did
390 not influence how diurnal or nocturnal daily bear movements were, bears moved primarily in
391 the nocturnal and twilight hours and less during daytime in areas with higher road density,
392 compared to areas with no roads (Ordiz et al. 2014). In fact, roads have many negative effects
393 on wildlife, e.g., causing direct mortality and favoring human activity (e.g., Trombulak and
394 Frissell 2000), and the road network is indeed an impediment for Scandinavian bear
395 movements (Bischof et al. 2017). Nevertheless, in the present study, we worked in an area
396 with high and very constant gravel road density, and this lack of variation likely explains the
397 relatively low magnitude of the road effect on the bears' flight responses.
398 Bears moved more often from their initial sites when approached in the berry season (≥ 15
399 July), a period when bears spend most time foraging ("hyperphagia") and human activity
400 levels are generally higher, than in the pre-berry season (Table 2), when the bear mating
401 season occurs and there are fewer human activities outdoors (Ordiz et al. 2011). Previous
402 research in Sweden has also shown that the bears' behavioral reactions are accentuated in
403 summer, compared to spring. For instance, bears seek denser vegetation cover in summer to
404 avoid human activities, including hunting (Ordiz et al. 2011, Ordiz et al. 2012). Number of

observers was important for whether the bears stayed or moved away and for DM. The effects of human disturbance on wildlife reflect perceived predation risk, which has often been shown to vary, as in our case, with factors such as the distance between humans and animals and with the number of humans causing disturbance (Beale and Monaghan 2004b).

We do not claim that the observed flight responses by the bears in Fennoscandia provide a full picture of their perceived predation risk. For instance, in the absence of visible behavioral responses, physiological responses have been documented for several species (e.g., Fowler 1999). Stress can cause a reduction in fitness, which can be due to higher metabolic needs in response to increased heart rate after disturbance (e.g., Beale and Monaghan 2004b). In Sweden, previous research has shown that bears have higher stress levels, measured in terms of heart rate variability, when they are closer to people than when they are farther away (Støen et al. 2015). Bears also change daily movement patterns for several days after disturbance, therefore altering optimal foraging and resting times (Ordiz et al. 2013).

As in previous studies (Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2015), we experienced no aggressive reactions by bears towards the observers, neither in Sweden nor in Finland, reinforcing the pattern of human avoidance by European brown bears. At the fine scale, bears rely on vegetation concealment or flee (Moen et al. 2012, Sahlén et al. 2015, this study) and at the landscape scale, bears spend most of the time far from human settlements (Nellemann et al. 2007).

Our study in Fennoscandia includes the lowest human densities across the distribution range of brown bears in Europe, but bear populations also thrive in eastern and southern Europe with much higher human densities (Swenson et al. 2000). Although bears and other large carnivores are generally elusive, as described above, behavioral reactions to approaching humans might differ if encounters occur more often, as they may do in areas with a higher human population and outdoor activity elsewhere than in Fennoscandia. Our results provide

important knowledge about bear reactions encountering people in the forest, but similar studies might be needed in other areas to reveal potential differences and similarities in large carnivore behavior when facing different human densities, activities and alternative management scenarios; e.g., bears are hunted in several European countries, but they are protected in southern Europe (Swenson et al. 2000).

Management implications

With expanding bear populations, bears are expected to settle closer to humans, and an important message to managers is that the bears' behavior to approaching humans does not seem to change solely based on the density of humans or roads in the bears' home ranges. Also, the lack of aggressive reactions by bears to observers on one hand, and the effects of human disturbance on bear behavior, which may cause fitness reduction as the ultimate cost of disturbance (Gill et al. 2001), on the other hand, are important messages for managers. In human-dominated landscapes, conservation-oriented management of large carnivores under hunting regimes, such as bears in Sweden and Finland, should aim to quantify and eventually account for the subtle, indirect effects of hunting and other human activities that cause disturbance, in addition to pay attention to more intuitive, lethal demographic effects (Frank et al. 2017, Bischof et al. 2018).

Acknowledgements

The study was conducted within the Scandinavian Brown Bear Research Project (SBBRP), which has primarily been funded by the Swedish Environmental Protection Agency, the Norwegian Environment Agency, the Austrian Science Fund, and the Swedish Association for Hunting and Wildlife Management. The study in Finland was funded by Jenny and Antti Wihuri, Ella and Georg Ehrnrooth, Kone and Oskar Öflund foundations, and grants to Janne Sundell. We thank the field personnel in SBBRP and at Finnish Game and Fisheries Research

Institute (currently Natural Resources Institute Finland) for assistance in field, Stefan Blumentrath for assistance with spatial analysis and John Stuiver for advice on spatial data handling. The reviews provided by Joacim Näslund and Ladislav Paule improved our original manuscript, which was reviewed in the frame of Peerage of Science. This is publication number 256 from the SBBRP.

References

Arnemo, J. M., Å. Fahlman, P. Ahlqvist, R. Andersen, H. Andrén, S. Brunberg, A. Landa, O. Liberg, J. Odden, J. Persson, P. Segerström, and J. E. Swenson. 2007. Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Norwegian School of Veterinary Science, Tromsø, Norway.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management **74**:1175-1178.

Barton, K. 2017. MuMIn: Multi-Model Inference. R package version 1.40.0.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1-48.

Beale, C. M., and P. Monaghan. 2004a. Behavioural responses to human disturbance: a matter of choice? Animal Behaviour **68**:1065-1069.

Beale, C. M., and P. Monaghan. 2004b. Human disturbance: people as predation-free predators? Journal of Applied Ecology **41**:335-343.

Bischof, R., C. Bonenfant, I. M. Rivrud, A. Zedrosser, A. Friebe, T. Coulson, A. Mysterud, and J. E. Swenson. 2018. Regulated hunting re-shapes the life history of brown bears. Nature Ecology and Evolution **2**:116-123.

Bischof, R., S. M. J. G. Steyaert, and J. Kindberg. 2017. Caught in the mesh: roads and their network-scale impediment to animal movement. Ecography **40**:1369-1380.

Bischof, R., J. E. Swenson, N. G. Yoccoz, A. Mysterud, and O. Gimenez. 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. Journal of Animal Ecology **78**:656-665.

Blumstein, D. T., L. L. Anthony, R. Harcourt, and G. Ross. 2003. Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? Biological Conservation **110**:97-100.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. A practical information-theoretic approach. 2nd edition. Springer, New York, USA.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling **197**:516-519.

Calenge, C. 2015. Home range estimation in R: the adehabitatHR package. https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf

Dahle, B., and J. E. Swenson. 2003. Home ranges in adult Scadinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. Journal of Zoology **260**:329-335.

Deecke, V. B., P. J. B. Slater, and J. K. B. Ford. 2002. Selective habituation shapes acoustic predator recognition in harbour seals. Nature **420**:171-173.

Dettki, H., G. Ericsson, T. Giles, and M. Norrsken-Ericsson. 2013. Wireless Remote Animal Monitoring (WRAM) - A new international database e-infrastructure for telemetry sensor data from fish

and wildlife. p. 247-256. In: Proceedings Etc 2012: Convention for Telemetry, Test Instrumentation and Telecontrol (Eds. The European Society of Telemetry). Books on Demand, pp. 292, ISBN: 978-3-7322-5646-4.
Eager, C. D. 2017. standardize: Tools for standardizing variables for regression in R. R package version 0.2.1.
ESRI. 2012. ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands, CA.
Eurostat. GEOSTAT 1km^2 population grid for 2006. http://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/population-distribution-demography/.
Finnish Meteorological Institute. Temperature and precipitation statistics from 1961 onwards. http://en.ilmatieteenlaitos.fi/statistics-from-1961-onwards.
Fowler, G. S. 1999. Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. Biological Conservation **90**:143-149.
Fox, J., and S. Weisberg. 2011. An {R} Companion to Applied Regression. 2nd edition. Sage, Thousand Oaks, CA.
Frank, S. C., A. Ordiz, J. Gosselin, A. Hertel, J. Kindberg, M. Leclerc, F. Pelletier, S. M. J. G. Steyaert, O.-G. Støen, J. Van de Walle, A. Zedrosser, and J. E. Swenson. 2017. Indirect effects of bear hunting: a review from Scandinavia. Ursus **28**:150-164.
Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology **6**:11.
George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation **133**:107-117.
Gibeau, M. L., A. P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. Biological Conservation **103**:227-236.
Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation **97**:265-268.
Gill, J. A., W. J. Sutherland, and A. R. Watkinson. 1996. A method to quantify the effects of human disturbance on animal populations. Journal of Applied Ecology **33**:786-792.
Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challanges and solutions. Journal of Evolutionary Biology **24**:699-711.
Kojola, I., and S. Heikkinen. 2006. The structure of the expanded brown bear population at the edge of the Finnish range. Annales Zoologici Fennici **43**:258-262.
Kopatz, A., H. G. Eiken, J. Aspi, I. Kojola, C. Tobiassen, K. F. Tirronen, P. I. Danilov, and S. B. Hagen. 2014. Admixture and gene flow from Russia in the recovering northern European brown bear (*Ursus arctos*). Plos One **9**:e97558.
Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience **48**:25-34.
Matson, G., L. Van Daele, E. Goodwin, L. Aumiller, H. Reynolds, and H. Hristienko. 1993. A laboratory manual for cementum age determination of Alaska brown bear first premolar teeth. Matson's Laboratory, Milltown, Montana, USA.
Moe, T. F., J. Kindberg, I. Jansson, and J. E. Swenson. 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). Canadian Journal of Zoology **85**:518-525.
Moen, G. K., O.-G. Støen, V. Sahlén, and J. E. Swenson. 2012. Behaviour of solitary adult Scandinavian brown bears (*Ursus arctos*) when approached by humans on foot. Plos One **7**:e31699.
Montgomery, D. C. 2005. Introduction to statistical quality control. 5th edition. Wiley, New York, USA.
National Land Survey of Finland. Terrängkarta 1:100,000. https://tiedostopalvelu.maanmittauslaitos.fi/tp/kartta?lang=sv.
National Veterinary Institute. 2017. Licensjakt på björn. http://sva.se/djurhalsa/vilda-djur/stora-rovdjur/licensjakt_pa_bjorn.

Naves, J., T. Wiegand, E. Revilla, and M. Delibes. 2003. Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. Conservation Biology **17**:1276-1289.

Nellemann, C., O.-G. Støen, J. Kindberg, J. E. Swenson, I. Vistnes, G. Ericsson, J. Katajisto, B. P. Kaltenborn, J. Martin, and A. Ordiz. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. Biological Conservation **138**:157-165.

Nielsen, S. E., M. S. Boyce, and G. B. Stenhouse. 2004. Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. Forest Ecology and Management **199**:51-65.

Ordiz, A., J. Kindberg, S. Sæbø, J. E. Swenson, and O.-G. Støen. 2014. Brown bear circadian behavior reveals human environmental encroachment. Biological Conservation **173**:1-9.

Ordiz, A., O.-G. Støen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia **166**:59-67.

Ordiz, A., O.-G. Støen, L. G. Langebro, S. Brunberg, and J. E. Swenson. 2009. A practical method for measuring horizontal cover. Ursus **20**:109-113.

Ordiz, A., O.-G. Støen, S. Sæbø, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they are being hunted? Biological Conservation **152**:21-28.

Ordiz, A., O.-G. Støen, S. Sæbø, V. Sahlén, B. E. Pedersen, J. Kindberg, and J. E. Swenson. 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. Journal of Applied Ecology **50**:306-314.

Ordiz, A., S. Sæbø, J. Kindberg, J. E. Swenson, and O.-G. Støen. 2017. Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? Animal Conservation **20**:51-60.

Pulliainen. 1983. Behaviour of an expanding population of the brown bear (Ursus arctos) in northern Europe. Z. Säugetierkunde **48**:290-297.

R Core Team. 2018. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria.

Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. Ecology **87**:2636-2646.

Sahlén, V., A. Ordiz, J. E. Swenson, and O. G. Støen. 2015. Behavioural differences between single Scandinavian brown bears (*Ursus arctos*) and females with dependent young when experimentally approached by humans. Plos One **10**:e0121576.

Sahlén, V., Swenson, J .E., Brunberg, S., Kindberg, J. 2006. Björnen i Sverige. A report from the Scandinavian Brown Bear Research Project to the Swedish White Paper on Predator Management, Stockholm, Sweden.

Solberg, K. H., E. Bellemain, O.-M. Drageset, P. Taberlet, and J. E. Swenson. 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. Biological Conservation **128**:158-168.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation **141**:2159-2173.

Statistics Finland. 2008. Statistical Yearbook of Finland 2008. Multiprint Oy, Finland.

Statistics Sweden. Population density per sq. km, population and land area by region and sex. Year 1991 - 2017. http://www.statistikdatabasen.scb.se/pxweb/en/ssd/START__BE__BE0101__BE0101C/BefArealTathetKon/?rxid=ac8a9f3d-fc94-4c9f-b33e-a5fbf8d4c8ab.

Statistics Sweden. Öppna geodata för tätorter. http://www.scb.se/hitta-statistik/regional-statistik-och-kartor/geodata/oppna-geodata/tatorter/.

Steyaert, S. M. J. G., A. Zedrosser, M. Elfström, A. Ordiz, M. Leclerc, S. C. Frank, J. Kindberg, O.-G. Støen, S. Brunberg, and J. E. Swenson. 2016. Ecological implications from spatial patterns in human-caused brown bear mortality. Wildlife Biology **22**:144-152.

601 Støen, O.-G., A. Ordiz, A. L. Evans, T. G. Laske, J. Kindberg, O. Fröbert, J. E. Swenson, and J. M.
602 Arnemo. 2015. Physiological evidence for a human-induced landscape of fear in brown bears
603 (*Ursus arctos*). Physiology & Behavior **152**:244-248.
604 Sundell, J., I. Kojola, and I. Hanski. 2006. A new GPS-GSM-based method to study behavior of brown
605 bears. Wildlife Society Bulletin (1973-2006) **34**:446-450.
606 Swedish Meteorological and Hydrological Institute. 2017a. Normal medeltemperatur för januari.
607 http://www.smhi.se/klimatdata/meteorologi/temperatur/normal-medeltemperatur-for-
608 januari-1.3976.
609 Swedish Meteorological and Hydrological Institute. 2017b. Normal medeltemperatur för juli.
610 http://www.smhi.se/klimatdata/meteorologi/temperatur/normal-medeltemperatur-for-juli-
611 1.3991.
612 Swedish National Land Survey. Fastighetskartan. https://www.lantmateriet.se/sv/Kartor-och-
613 geografisk-information/Kartor/Fastighetskartan/
614 Swedish National Land Survey. Vägkartan. https://www.lantmateriet.se/sv/Kartor-och-geografisk-
615 information/Kartor/Vagkartan/.
616 Swenson, J. E., N. Gerstl, B. Dahle, and A. Zedrosser. 2000. Action plan for the conservation of the
617 brown bear in Europe (*Ursus arctos*). Strasbourg Cedex, Council of Europe. Nature and
618 environment.
619 Swenson, J. E., F. Sandegren, and A. Söderberg. 1998. Geographic expansion of an increasing brown
620 bear population: evidence for presaturation dispersal. Journal of Animal Ecology **67**:819-826.
621 Swenson, J. E., M. Schneider, A. Zedrosser, A. Söderberg, R. Franzén, and J. Kindberg. 2017.
622 Challenges of managing a European brown bear population; lessons from Sweden, 1943–
623 2013. Wildlife Biology **2017**:wlb.00251.
624 Swenson, J. E., P. Wabakken, F. Sandegren, A. Bjärvall, R. Franzén, and A. Söderberg. 1995. The near
625 extinction and recovery of brown bears in Scandinavia in relation to the bear management
626 policies of Norway and Sweden. Wildlife Biology **1**:11-25.
627 Tablado, Z., and L. Jenni. 2017. Determinants of uncertainty in wildlife responses to human
628 disturbance. Biological Reviews **92**:216-233.
629 The Finnish Wildlife Agency. 2017. Karhusaaliit.
630 https://riista.fi/metsastys/saalisseuranta/karhusaaliit/.
631 Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and
632 aquatic communities. Conservation Biology **14**:18-30.
633 Vincze, E., S. Papp, B. Preiszner, G. Seress, V. Bókony, and A. Liker. 2016. Habituation to human
634 disturbance is faster in urban than rural house sparrows. Behavioral Ecology **27**:1304-1313.
635 Whittaker, D., and R. L. Knight. 1998. Understanding wildlife responses to humans. Wildlife Society
636 Bulletin **26**:312-317.
637 Wikman, M. 2010. Riistakannat 2010. Riistaseurantojen tulokset. Riista- ja kalatalouden
638 tutkimuslaitos, Helsinki, Finland.
639 Zedrosser, A., S. M. J. G. Steyaert, H. Gossow, and J. E. Swenson. 2011. Brown bear conservation and
640 the ghost of persecution past. Biological Conservation **144**:2163-2170.
641 Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and
642 extensions in ecology with R. Springer Science+Business Media, New York, USA.
643

644 **Appendix 1**

645 Sets of top candidate models, with ΔAICc < 2 compared to the model with the lowest AICc for each
646 response variable, for flight reactions of brown bears experimentally approached in southcentral
647 Sweden.

648
649 Table 1A: Best candidate models (ΔAICc < 2) following generalized linear mixed regression
650 (binominal link function) explaining the factors that influenced whether brown bears stayed (0) or
651 moved away (1) when approached by humans in southcentral Sweden, from 2006 to 2009 (n = 118).
652 The continuous variables were scaled to 1 SD. See Table 1 for explanation of the variables.
653

Model	AICc	ΔAICc	weight
Season + Number of observers	134.41	0.00	0.21
Season + Number of observers + Distance to observer	134.99	0.58	0.16
Season + Number of observers + Human HR	135.24	0.83	0.14
Season + Number of observers + Road HR	135.49	1.08	0.12
Season + Number of observers + Distance to observer + Human HR	135.94	1.53	0.10
Season + Number of observers + Distance to road from IS	136.11	1.70	0.09
Season + Number of observers + Distance to observer + Road HR	136.18	1.78	0.09
Season + Number of observers + Activity	136.21	1.80	0.09

654
655
656 Table 2A. The best candidate models (ΔAICc < 2) following linear mixed regression explaining
657 distance moved (DM) for bears when approached by humans in southcentral Sweden from 2006 to
658 2009 (n = 71). The bears left their initial sites before the observers passed them. DM is log
659 transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the variables.
660

Model	AICc	ΔAICc	weight
Activity + Sex + Sighting distance in IS + Number of observers	202.93	0.00	0.55
Activity + Sighting distance in IS + Number of observers	204.51	1.58	0.25
Activity + Sex + Sighting distance in IS + Number of observers + Season	204.87	1.94	0.21

661
662
663 Table 3A. The best candidate models (ΔAICc < 2) following linear mixed regression explaining time
664 spent moving after disturbance (TSM) for bears when approached by humans in southcentral Sweden
665 from 2006 to 2009 (n = 63). The bears left their initial sites before the observers passed them. TSM is
666 log transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the
667 variables.
668

Model	AICc	ΔAICc	weight
Number of observers	167.62	0.00	0.37
Number of observers + Sighting distance in IS	168.31	0.68	0.26
NULL	168.74	1.12	0.21
Number of observers + Sex	169.26	1.64	0.16

669